Personality Dimensions and Their Behavioral Correlates in Wild Virunga Mountain Gorillas (*Gorilla beringei* *beringei*)

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ACKNOWLEDGEMENTS

We thank the Rwandan government and the Rwandan Development Board for their long-term support of the research and protection activities of the Karisoke Research Center. We are indebted to all Karisoke research and field assistants who contributed to the completion of the personality questionnaires and the long-term behavioral database as well as to K. Fawcett for assistance and comments at an early stage of the project. For translation of the personality questionnaire into French we thank M. Lherbier.

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Abstract

Studies of animal personality improve our understanding of individual variation in measures of life-history and fitness, such as health and reproductive success. Using a 54 trait personality questionnaire developed for studying great apes and other nonhuman primates, we obtained ratings on 116 wild mountain gorillas (*Gorilla beringei beringei*) monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center in Rwanda. There were eight raters who each had more than 1.5 years of working experience with the subjects. Principal component analyses identified four personality dimensions with high inter-rater reliabilities --- Dominance, Openness, Sociability, and Proto-Agreeableness --- that reflected personality features unique to gorillas and personality features shared with other hominoids. We next examined the associations of these dimensions with independently collected behavioral measures derived from long-term records. Predicted correlations were found between the personality dimensions and corresponding behaviors. For example, Dominance, Openness, Sociability, and Proto-Agreeableness were related to gorilla dominance strength, time spent playing, rates of approaches and rates of interventions in intra-group conflicts, respectively. These findings enrich the comparative-evolutionary study of personality and provide insights into how species differences in personality are related to ecology, social systems, and life history.

Keywords: Personality, mountain gorillas, wild, evolution, behavior

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Comparative Personality Research

The study of animal personality, that is stable individual differences in behavior within populations (Freeman & Gosling, 2010), has become a growing area of research in behavioral ecology (Réale, Dingemanse, Kazem, & Wright, 2010) and comparative psychology (Gosling, 2001). This increased interest stems largely from a desire to understand the adaptive significance of behavioral phenotypes in numerous animal populations (Réale at al., 2010; Kralj-Fiser & Schuett, 2014). More specifically, for those studying the adaptive function of personality, there is a need to address the vexing question of why additive genetic variation in personality persists in spite of the fact that personality dimensions are associated with fitness-related outcomes (Penke, Denissen, & Miller, 2007)? A related question concerns why individual differences in behavioral, affective, and cognitive dispositions can be described by a few broad species-typical dimensions in humans (Goldberg, 1990), nonhuman great apes, and other primates (Freeman & Gosling, 2010).

Examining which traits make up the smaller number of personality dimensions in different species is useful for understanding the phylogeny of personality (Gosling & Graybeal, 2007). For instance, studies of chimpanzees (King & Figueredo, 1997) and orangutans (Weiss, King, & Perkins, 2006) have been used to trace the origins of human dimensions—Openness, Conscientiousness, Extraversion, Agreeableness, and Neuroticism—known as the "Big-Five" or "Five-Factor Model" (Digman, 1990; Goldberg, 1990). From the study of chimpanzee personality structure, which resembled the human Big-Five with the addition of a dimension related to dominance and competitive prowess (King & Figueredo, 1997), the most parsimonious

explanation is that the five human factors were present in the common ancestor of humans and chimpanzees ~4-6 million years ago. Likewise, the study of orangutan personality indicated that Neuroticism, Extraversion, and Agreeableness can be traced to the common ancestor of great apes ~15-16 million years ago, and that dimensions describing the common ancestor of great apes also included a dimension related to competitive prowess and one that included tendencies towards decisiveness, intelligence, and competence (Weiss et al., 2006).

Comparing dimensions that describe multiple personality traits across species requires the assessment of these dispositions using comparable methods. One approach is to obtain ratings of personality traits from knowledgeable judges. The validity of this method is well-accepted as ratings are consistent across independent judges (Gosling, 2001), stable over time and contexts (Capitanio, 1999; King, Weiss, & Sisco, 2008; Weiss, Adams, Widdig, & Gerald, 2011), associated with physiological characteristics and health (Blatchley & Hopkins, 2010; Capitanio, Mendoza, & Bentson, 2004; Capitanio, Mendoza, & Cole, 2011; Locurto, 2007; Weiss, Gartner, Gold, & Stoinski, 2012), well-being (King & Landau, 2003; Weiss et al., 2006; Weiss, Adams, Widdig, & Gerald, 2011), and observed behaviors (Gold & Maple, 1994; Gosling & Vazire, 2002; Konečná et al., 2008; Konečná, Weiss, Lhota, & Wallner, 2012; Kuhar, Stoinski, Lukas, & Maple, 2006; Morton, Buchanan-Smith, Brosnan, Thierry, & Paukner, 2013; Pederson, King, & Landau, 2005; Schaefer & Steklis, 2014). Moreover, chimpanzee personality dimensions described by raters from different cultures on different populations of the same species reveal highly similar dimensions (King, Weiss, & Farmer, 2005; Weiss et al., 2009; Weiss, King, & Hopkins, 2007), and there is mounting evidence that these dimensions are genetically-based (Adams, King, & Weiss, 2012; Hong et al., 2011; Hopkins, Donaldson, & Young, 2012; Weiss,

King, & Figueredo, 2000), and not the products of rater biases, including anthropomorphic projection (Weiss et al., 2012).

Study objectives

The first two goals of this study were to describe wild mountain gorilla personality and to compare it to the personalities of chimpanzees (King & Figueredo, 1997), orangutans (Weiss, King, & Perkins, 2006), rhesus macaques (Weiss et al., 2011), and brown capuchin monkeys (Morton et al., 2013), all of which were assessed using the Hominoid Personality Questionnaire (HPQ; Weiss et al., 2009). To these ends, while previous studies of gorilla personality (Gold & Maple, 1994; Kuhar et al., 2006) used the Gorilla Behavioral Index, a modified version of the Madingley Questionnaire (Stevenson-Hinde & Zunz, 1978), we used a modified version of the HPQ so that we could directly compare the dimensions of mountain gorillas to those of the other species.

The third goal of this study was to examine sex and age differences in mountain gorilla personality. Gorillas are the most sexually dimorphic great ape (Taylor, 1997) as a result of strong sexual selection among males who compete for access to reproductive females (Harcourt & Stewart, 2007). We hypothesize that such high sexual dimorphism in gorillas leads to sex differences in personality, which become more evident in adulthood when sexual differentiation has complete.

The fourth goal of this study was to examine the association between gorilla personality dimensions and naturally occurring behaviors. A previous study of 25 captive gorillas, using the Gorilla Behavioral Index (Kuhar et al., 2006), found modest correlations between behaviors and personality dimensions labeled extroverted, dominant, fearful, and understanding. More recently, in six captive male gorillas, Schaefer and Steklis (2014) found associations between behaviors

and personality dimensions labeled Dominance, Extraversion/Agreeableness, and Conscientiousness that were obtained from ratings on the HPQ in ways consistent with the definitions of these dimensions. Because these previous gorilla studies were constrained by behaviors observed in zoo settings, we aimed to test predictions for a large sample of wild gorillas on the relationship between specific naturally occurring gorilla behaviors and the personality dimensions that emerged from the HPQ.

Which dimensions characterize mountain gorilla personality?

We used multiple approaches for predicting personality features of the Virunga mountain gorillas. Specifically, we focused on gorilla-specific and population-specific ecology and social system. We also considered existing findings in great apes (Weiss et al., 2011) and the 14 most commonly identified personality categories in primates across 18 comprehensive studies (see Table II in Freeman & Gosling, 2010).

Among great apes and within gorillas, the Virunga mountain gorillas comprise the most folivorous population (Harcourt & Stewart, 2007). Their high-altitude habitat represents an extreme for the genus and is characterized by low fruit availability but dense terrestrial vegetation that is spatially and temporally abundant (Fossey & Harcourt, 1977; Schaller, 1963; Vedder, 1984; Watts, 1984). These environmental conditions translate into low levels of intra- and inter-group food competition (Robbins, Robbins, Gerald-Steklis, & Steklis, 2007), which is reflected in relatively low levels of intra-group aggression and large home range overlaps between groups (Caillaud et al., 2014; Fossey & Harcourt, 1977; Harcourt & Stewart, 2007). This pattern differs considerably from other great ape populations (Harcourt & Stewart, 2007). We hypothesize that living in such a stable and predictable environment with limited food competition results in low vulnerability to stress, low aggressiveness, high emotional stability,

and very low neurotic tendencies. This hypothesis is further supported by the general nature of gorillas which is commonly described as calm, introverted and emotionally stable (Parker & Mitchel, 1999).

In addition, in a stable environment such as the Virunga habitat, curiosity, creativity and exploratory tendencies may not be as necessary as in environments with seasonal food shortages. As a consequence, mountain gorillas may not have experienced strong selection to explore alternative food sources and food extraction techniques, such as hunting and termite fishing in chimpanzees, to ensure their survival (Boesch & Boesch, 1989, 1990). This has been offered as an explanation for why Openness is absent in Hanuman langurs (Konečná et al., 2008, though see Konečná et. al., 2012). Thus, from an ecological perspective, we expect mountain gorillas to lack a personality dimension incorporating curiosity, creativity, and exploration, such as Openness in humans (Goldberg, 1990) and chimpanzees (King & Figueredo, 1997). On the other hand, Openness may be important in adult gorilla personality from a social standpoint. Dispersal pattern strategies to avoid inbreeding and to increase breeding opportunities set gorillas apart from other great apes because emigration from the natal group is common for both sexes (Robbins, 1995; Watts, 1990). Females transfer during inter-group encounters, whereas males become solitary after leaving their natal group and then attempt to recruit females from existing groups. Both situations require individuals to be socially curious and open, and thus from a social perspective adult gorillas should have a dimension reflecting Openness.

Gorillas live in hierarchically structured societies with adult males clearly dominant over females (Harcourt & Stewart, 2007). Dominance hierarchies within the sexes also exist, although female-female relationships are generally considered more egalitarian than in other primates as a result of the lower levels of feeding competition (Robbins, 1996; Robbins, Robbins, Gerald-

Steklis, & Steklis, 2005). Accordingly, we predict that mountain gorilla personality will be characterized by a Dominance dimension and that adult males score higher than adult females on such a dimension, with stronger sex differences in adulthood. Dimensions categorized as Confidence, Independence and Intelligence (Freeman & Gosling, 2010) complement qualities associated with dominance in mountain gorillas and thus should be closely tied to gorilla Dominance in a similar fashion to that shown in other nonhuman great apes (Gold & Maple, 1994; King & Figueredo, 1997; Kuhar et al. 2006; Schaefer & Steklis, 2014).

The social role of male and female gorillas is also distinct (Harcourt & Stewart, 2007). Silverbacks, in particular dominant males, act as group leaders, mediate within-group social conflicts, and protect infants from infanticide (Schaller, 1963; Harcourt & Stewart, 2007; Watts, 1989). This role requires supportive attitudes that are commonly part of an Agreeableness dimension in humans and other great apes (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2009; Weiss et al., 2006). Females, on the other hand, are compliant and rely on male protection and leadership. Females also cooperate with each other in contests by supporting subordinate parties (Harcourt & Stewart, 2007). Thus, gorillas are expected to show an Agreeableness dimension.

Compared to other great apes, gorillas form cohesive social groups without regular fission-fusion dynamics (Harcourt & Stewart, 2007). In addition, between- rather than within-sex relationships form the core of gorilla society (Harcourt, 1979; Watts, 1992, 1996) as females establish and maintain bonds with males (Harcourt & Stewart, 2007; Watts, 1992). Thus, a distinct Sociability dimension on which adult females score higher than males is expected in gorilla personality structure. Table 1 summarizes our predictions for the personality structure of the Virunga mountain gorilla based on key ecological and social features.

Insert Table 1 about Here

Methods

Subjects

Subjects were 116 wild habituated Virunga mountain gorillas (60 females and 56 males; Table 2) monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center in the Volcanoes National Park, Rwanda. The mean age of subjects was 13.5 years (*SD* = 9.7). Female and male gorillas had a mean age of 15.4 years (*SD* = 10.5) and 11.1 years (*SD* = 8.2), respectively.

Insert Table 2 about Here

Ratings

Questionnaire. Personality was assessed using a version of the HPQ (Weiss et al., 2009) modified for studying wild mountain gorillas (HPQ_{GO}) (see supplemental questionnaire). For the purpose of this study, the HPQ_{GO} was provided in English and French. The HPQ_{GO} includes 54 traits selected from measures and taxonomies of the human Five-Factor Model (Goldberg, 1990) and later additions (see supplemental Table 1). Each trait was paired with a brief description that set it in the context of wild mountain gorilla behavior. The HPQ_{GO} instructs raters to base their ratings on whether a gorilla scores above, below, or average for a trait on their "own subjective judgement of typical gorilla behavior" (see supplemental questionnaire) rather than on estimated frequencies of particular behaviors. Raters were instructed to avoid discussing their ratings and

to rate each trait on a 7-point scale, ranging from trait displayed "either total absence or negligible amounts" (1) to "extremely large amounts" (7).

Raters and Rating Procedure. There were eight raters, each with more than 1.5 years of working experience with this population (M = 9.6 years) and training in collecting long-term behavioral data. This led to a total of 556 ratings of the 116 gorillas (M = 4.8 raters per gorilla). Ratings took place between June 2007 and January 2008. Raters completed the HPQ_{GO} for individual gorillas they had known for at least one year. Thus, infants younger than one year were excluded from the study.

Six Rwandan raters used the French translation of the HPQGO and two international researchers used the English version. Completion of the questionnaire differed slightly between English- and Rwandan-speaking raters. English-speaking raters completed the questionnaire individually, whereas Rwandan raters met as a group and rated each gorilla in assistance of a professional Rwandan translator with a Bachelor's degree in French and English. The group setting allowed brief clarifications of the rating concept and French trait definitions in their native language, Kinyarwanda, to ensure that potential language barriers had a minimal influence on the understanding of each trait. During those meetings, raters were not allowed to discuss their rating decisions and experiences related to the gorillas.

Behavioral Data Collection. Ten researchers at the Karisoke Research Center, including four who rated gorilla personality, collected long-term behavioral data (see Table 3). Before researchers started collecting behavioral data, inter-observer reliability tests were conducted with occasional follow-ups to ensure the reliability of these data. The data set incorporates behavioral records from up to two years prior to subjects' rating age; for example, ratings on an eight year-old gorilla would be validated with behavior collected between the gorilla's sixth and eighth year

of life. Data from focal animal samples provided a mean of 23 hours (*SD* = 17) of observation time per gorilla and a total of 2,691 hours. The majority of behavioral data were recorded continuously (see Table 3). Activity patterns of the focal animal and social group, as well as proximity data (number of individuals within 5 m distance) of the focal animal were recorded using instantaneous sampling with 5-min or 10-min sampling intervals. We distinguished group resting from group non-resting states (feeding, feed-travel, and travel).

Insert Table 3 about Here

Analyses

Missing Data. One rater omitted five trait ratings across three gorillas. Those missing values were substituted with the mean ratings for those traits over all other raters.

Trait Inter-rater Reliabilities. Because we were only interested in the reliabilities of those raters who were familiar with these gorillas, inter-rater reliabilities of ratings were determined using two intraclass correlations (*ICC*s) that treat raters as a fixed effect (Shrout & Fleiss, 1979). The first, *ICC*(3,1), indicates the reliability of individual ratings of the raters. The second, *ICC*(3,*k*), indicates the reliability of mean ratings across raters.

These *ICC*s were computed using mean squares derived from a general linear model in which the score assigned to a particular trait is the dependent variable. The predictors in this model include categorical variables representing the target (gorilla), the judge (rater), and the Target × Judge interaction. The mean square for the first predictor term is the between targets mean square (BMS) and indicates the amount of variance contributed by the target. The mean square for the second predictor term is the error mean square (EMS) and indicates the amount of

variance contributed by the error. *ICC*(3,1) is equal to the ratio of the difference between BMS and EMS to the sum of BMS and the product of EMS and (*k*-1) where *k* equals the mean number of raters per subject. *ICC*(3,*k*) is equal to the ratio of the difference between BMS and EMS to BMS.

We excluded traits with *ICC*s ≤ 0 from further analyses. This liberal cut-off point was chosen to be consistent with prior studies and recommendations (Gosling & Vazire, 2002; Weiss et al., 2009), and because, for any measure of reliability, single traits have markedly lower reliabilities than scales (see Nakagawa & Schielzeth, 2010, equation 37 or Nunnally & Bernstein, 1994, equations 6-18).

Identifying Personality Structure. For each gorilla we took the mean trait scores across raters for all reliable traits and analyzed these scores using principal-components analysis (PCA). We used Horn's (1965) parallel analysis to determine the number of components that had eigenvalues exceeding the eigenvalue expected under chance at the 95th percentile. We rotated components using orthogonal (varimax) and oblique (promax) procedures. If the oblique rotation produced components that were highly intercorrelated or noticeably different from those derived using the orthogonal rotation, we retained the components from the oblique solution. We otherwise retained the components from the orthogonal solution.

We next tested whether the dimensions identified were affected by the fact that the mean age of this sample was lower than that of the sample of chimpanzees (M = 18.7 years; SD = 12.0; King & Figueredo, 1997) and the sample of orangutans (M = 21.4; SD = 11.5; Weiss et al., 2006), both of which have comparable lifespans to gorillas. We first conducted two additional PCAs. The first was based on a subsample of 100 gorillas that were not infants (age > 3.5 years). The second was based on a subsample of 86 gorillas that included only subadults and adults (age

> 6 years). In both cases, as before, we used the same procedure to determine the number of components to select between the varimax- or promax-rotated components. We then compared the structures derived from these subsamples to that of the full sample using targeted orthogonal Procrustes rotations (McCrae, Zonderman, Bond, Costa, & Paunonen, 1996).

Finally, like previous studies that used this questionnaire (Morton et al., 2013; Weiss et al., 2006, Weiss et al., 2009, Weiss et al., 2011), trait loadings ≥ |.4| were defined as salient. In cases where two or more components had salient loadings on a trait, the trait was assigned to the component with the higher loading. We used these definitions to generate unit-weighted component scores (Gorsuch, 1983) in which traits with salient and positive loadings were assigned a weight of +1, traits with salient and negative loadings were assigned a weight of -1, and all other loadings were assigned a weight of 0. Unit weighted component scores were converted into z-scores.

Cross-species Comparisons. To identify, describe, and label personality dimensions, we compared the gorilla personality dimensions derived in this study to those derived in studies of other species that used the HPQ or one of its antecedents (see supplemental Table 1), i.e. the Chimpanzee Personality Questionnaire (King & Figueredo, 1997) or the Orangutan Personality Questionnaire (Weiss et al., 2006). We first computed unit-weighted scores for our sample based on the personality structures of chimpanzees (King & Figueredo, 1997; Weiss et al., 2009), orangutans (Weiss et al., 2006), rhesus macaques (Weiss et al., 2011), and brown capuchin monkeys (Morton et al., 2013). We then obtained correlations between these unit-weighted scores and those based on the gorilla structure identified in this study.

Component Reliabilities. We estimated *ICC*(3,1) and *ICC*(3,*k*) for each gorilla personality component in the same manner as we did for the traits. For each component, we also computed Cronbach's alpha, a measure of internal consistency reliability.

Age and Sex Differences. To investigate sex and age effects on mountain gorilla personality, we conducted individual linear regression models for each gorilla personality dimension (z-scores) with sex, age, and Sex × Age being entered as independent variables. Age was mean centered to facilitate the interpretation of interactions.

Behavioral Correlations. We used two-tailed Spearman's rank correlations to examine whether those mountain gorilla personality dimensions derived from ratings were associated with predicted behavioral observations (see Table 3). Construct validity was tested by linking behavior with personality dimensions to understand the functional bases of personality dimensions.

Since social behavior can be influenced by the predominant group activity (Harcourt, 1978), where appropriate, behaviors were analyzed separately by group activity (see Table 3). This approach accounts for unequal proportions of group resting and non-resting periods during focal sampling. For example, grooming occurs more frequently during group resting periods in mountain gorillas (Harcourt, 1978). Also, food-stealing is expected to occur more frequently when the majority of the group is feeding or feed-traveling. Similarly, our analysis of "time spent resting" and "number of individuals within 5 m" was restricted to group resting periods since a bias in data collection towards group non-resting periods is likely to translate into less time resting and fewer individuals in proximity, respectively.

We also calculated frequencies of each continuously collected behavior (except displacement and grooming) per total observation time (in hours). In the case of instantaneously collected proximity data, we calculated the mean number of individuals within 5 m over all scans for each gorilla. Instantaneous data on grooming, playing, and resting were transformed into the percentage of scans a gorilla spent in each of the activities. In addition, we counted the number

of grooming recipients of each gorilla as a measure of social network strength. To account for the availability of potential grooming partners, we used the number of group members each gorilla groomed, calculated as a percentage of total partners, for further statistical tests. Furthermore, the suitability of a behavior as an indicator of a given personality dimension can change with gorilla age. For example, grooming indicates sociability in adult gorillas better than in immature gorillas because social grooming of others is not common in mountain gorillas until adolescence (Fletcher, 1994). Hence, age effects on behaviors such as playing, grooming, aggression, and intervening in social conflicts, were taken into account by limiting the analyses to gorillas within the appropriate age range for those behaviors (see Table 3). Also, if a behavior was analyzed by group activity, we split the dataset by group activity before calculating frequencies, means, or percentages.

The dominance strength of adult gorillas was calculated from displacement events using the Wittemyer and Getz (2006) method, which is particularly appropriate for dominance matrices with unknown dyadic relationships. As a first step, matrices of adult female and adult male dominance relationships (established through displacements) for each study group (Pablo, Beetsme, and Shinda) were rearranged by minimizing the number of inconsistencies (I) and the strength of these inconsistencies (SI) using an iterative procedure ('I & SI method') following de Vries (1998), provided by Matman™ software version 1.0 (Noldus Information Technology, 1998). The order of two individuals, A and B, in a matrix is defined as inconsistent when A dominates B but A is below B. The strength of the inconsistency would be the distance between the ranks of A and B. Second, all unknown values a_{ij} for dyad ***i*** **-** ***j*** with ***i*** and ***j*** referring to reordered ranks (first step) were replaced with interpolated values $\hat{a}_{ij}$, calculated by equation 1 where N is the total number of males / females in a given hierarchy matrix:

$$\hat{a}_{ij} = (1 - \hat{a}_{ji}) = 0.5 - ((\boldsymbol{i} - \boldsymbol{j}) / 2N) \quad (1)$$

The interpolation is thus built upon the assumption that, the greater the separation in ranks between two individuals with an unknown relationship, the more likely the higher-ranking individual is to dominate the lower-ranking individual (Bradley & Terry, 1952; Crow, 1990). As a final step, to obtain a unique rank order for adult males and adult females in each study group, the relative dominance strength for each individual ***i*** was generated by subtracting the column sum (sum of losses) from the row sum (sum of wins) in the interpolated hierarchy matrix. Once the gorilla personality structure was described, we made predictions about the relationships between behavior measures and dimensions to evaluate convergent validity between both measures (see Results section).

Results

Inter-Rater Reliabilities of Traits

The *ICC*(3,1) and *ICC*(3,*k*) for each trait are presented in supplemental Table 2. One trait, *unperceptive*, was not reliable. *ICC*(3,1)s of the remaining traits ranged from .03 for *predictable* to .72 for *dominant* (*M* = .26, *SD* = .16). *ICC*(3,*k*)s of the remaining traits ranged from .14 for *predictable* to .92 for *dominant* (*M* = .58, *SD* = .20).

Principal Component Analyses

Parallel analyses indicated that there were four components in the full data set, five components in the subsample that did not include infants, and four components in the subsample that only included subadults and adults. To determine whether to retain a four or five component solution, we conducted an Everett (1983) test. This involved obtaining four and five component solutions from the full data set and the two subsamples. These solutions were then compared using targeted orthogonal Procrustes rotations (McCrae et al., 1996).

The four component solutions for the two subsamples were nearly equivalent to those derived from the full data set (see top panel of Table 4). However, while the five component solution for the subsample that did not include infants was nearly equivalent to the full data set, the fifth component from the sample that included subadults and adults was notably lower (see

bottom panel of Table 4). These results indicate that including infants and juveniles did not influence the component structure, and that the four component solution was the most stable. We therefore retained the four component solution of the full data set for further analyses.

Insert Table 4 about Here

Most communalities were high (> .6), only a few communalities were low (< .5), and the ratio of traits to dimensions was high. Therefore, our sample size was sufficient to guarantee a stable structure (de Winter, Dodou, & Wieringa, 2009; MacCallum, Widaman, Zhang, & Hong, 1999). The fact that all dimensions have at least four traits with loadings greater than |.6| also indicates that the structure is stable (Guadagnoli & Velicer, 1988).

The correlations among dimensions were modest with a range of .02 to .41 and a mean of .22, and there were only minor differences between the varimax- (see Table 5) and promax-rotated dimensions (see supplemental Table 3). We thus interpreted the varimax solution. The dimensions explained 68% of the variance.

Insert Table 5 about Here

Cross-Species Comparison

The first dimension most closely resembles the chimpanzee Dominance dimension (see Table 6) with 12 out of 18 shared trait loadings (see Table 5) (King & Figueredo, 1997; Weiss et al., 2009). We therefore labeled this gorilla dimension 'Dominance' (D_{GO}). However, D_{GO} differs from chimpanzee Dominance by lacking an aggressive-coercive facet and by including the traits

protective, *helpful*, and *sensitive* that load on the 'Agreeableness' dimension in humans (Goldberg, 1990), chimpanzees (King & Figueredo, 1997), and orangutans (Weiss et al., 2006). The D_{GO} dimension's similarity with orangutan Intellect reflects the common loading of *intelligent*, *independent*, and *decisive* on this dimension (Weiss et al., 2006). Finally, D_{GO} resembled the rhesus macaque Confidence and, to a lesser extent, brown capuchin monkey Assertiveness.

Insert Table 6 about Here

The second dimension is characterized by traits describing exploration, creativity, impulsivity, lack of caution, activity, and emotional instability (see Table 5). This dimension strongly resembles Openness in brown capuchin monkeys (Morton et al., 2013) and rhesus macaques (Weiss et al., 2011) (see Table 6), and to a lesser extent chimpanzee Openness (King & Figueredo, 1997; Weiss et al., 2009), which together support the interpretation of this second dimension as 'Openness' (O_{GO}). The O_{GO} facet that describes exploratory tendencies and creativity (*curious*, *inquisitive*, *innovative*, and *inventive*) is shared with brown capuchin monkeys (Morton et al., 2013), rhesus macaques (Weiss et al., 2011), humans (Goldberg, 1990), and chimpanzees (King & Figueredo, 1997). However, only mountain gorillas and brown capuchin monkeys integrate an activity facet comprising the traits *active*, not *lazy*, and *playful*, into Openness. In humans and great apes, this facet is commonly found in Extraversion (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2006). O_{GO} also includes traits reflecting impulsiveness and emotional instability (not *unemotional*, *impulsive*, *excitable*, not *stable*,

erratic, not *predictable*, and not *cool*) which load on Neuroticism across humans and other great apes (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2009; Weiss et al., 2006).

The third dimension describes *social*, *affectionate*, *gentle*, and *sympathetic* gorillas who were not *solitary*, not *depressed,* not defiant, and not *individualistic*. Six out of nine traits matched those defining Extraversion or Agreeableness in humans and other great apes (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2006; Weiss et al., 2009) (see Table 5). A combination of Extraversion and Agreeableness dimensions also emerged in the personality of rhesus macaques (Weiss et al., 2011) and brown capuchin monkeys (Morton et al., 2013), named Friendliness and Sociability, respectively (see Table 6). Given the closest resemblance of this gorilla dimension to the brown capuchin monkey Sociability dimension, and the absence of an activity facet tied to Sociability in gorillas as in the Extraversion dimension of other great apes, we labeled the third dimension Sociability (S_{GO}).

Likely on account of its high negative loadings on traits related to aggressive behavior and hostile emotions, the final gorilla dimension most closely resembles the inverse of the orangutan (Weiss et al., 2006) and rhesus macaque Dominance (Weiss et al., 2011) and was the mirror image of brown capuchin Assertiveness (Morton et al., 2013) (see Table 6). This dimension also marks traits capturing low Agreeableness in humans (Goldberg, 1990) and shares trait loadings of Conscientiousness in chimpanzees (Weiss et al., 2009) (see Table 5). The last gorilla dimension thus describes content, emotionally stable, and friendly gorillas. Since key traits from human Conscientiousness such as *organized*, *cautious*, *thoughtful*, and *persistent* were missing in this dimension, we labeled it ‘Proto-Agreeableness’ (P-AGO).

Component Inter-Rater Reliabilities and Internal Consistency Reliabilities

The inter-rater reliabilities of components ranged from moderate to substantial. The internal consistency reliabilities were all high (see Table 7).

Insert Table 7 about Here

Age and Sex Differences

The parameter estimates of the regression model (see Table 8) for the examination of age and sex effects on each gorilla personality dimension (see Figure 1) show that male gorillas had higher Dominance scores than female gorillas from approximately the age of 8 years with a significantly steeper age-related increase on D_{GO} in males compared to females. Males were also more open than females in particular until the age of 20 years but also displayed a steeper age-related decrease in Openness. Female gorillas, on the other hand, were more social than males. This sex difference was consistent across all ages. No sex differences occurred in the gorilla variant of Agreeableness which declined with age.

Insert Table 8 and Figure 1 about Here

Behavioral Validation

Predictions. Based on the gorilla personality structure, we made predictions for associations between behavioral measures (see Table 3) and each of the personality dimensions. We predicted D_{GO} would be related to the dominance strength in adult gorillas. We also expected a positive association between rates of interventions (per hour) and D_{GO} because a supportive facet characterizes this dimension.

Exploratory and investigative tendencies, as well as activity, are key facets of O_{GO} and thus this dimension should be positively associated with rates of staring (per hour) and playing (percentage of scans) and whilst negatively associated with resting (percentage of scans). Moreover, because staring and playing imply close proximity to interaction partners, we predicted a direct association between O_{GO} and rates of approach and the number of gorillas within 5 m.

S_{GO} is comprised of traits characterizing a social, agreeable, and peaceful gorilla, and is expected to correspond to social behavior such as staring, grooming (percentage of scans), and rate of touching (per hour). In addition, an inverse relationship was predicted between S_{GO} and rates of aggression (per hours). Because of the lack of an activity facet in $S_{GO,}$ we did not expect a correlation between this dimension and playing. Also, like O_{GO}, gorillas high on Sociability should have high rates of approach and high numbers of gorillas within 5 m to maintain an environment for social interaction.

We predicted a negative relationship between P-A_{GO}, which has negative loadings on the traits *manipulative* and *aggressive*, and both rates of aggression and rates of interventions, which usually involve aggressive elements. Low jealousy and stinginess that characterize higher scores on this dimension should be reflected in low rates of food-stealing (per hour).

Correlations Between Gorilla Behavior and Personality Dimensions. As expected, D_{GO} correlated positively with dominance strength in adult gorillas (see Figure 2) and rates of interventions (by subadults and adults) (see Table 9). We conducted an additional test with rates of interventions for males and females separately which showed a significant relationship between rates of interventions and D_{GO} scores in males ($N = 39$, $r_s = .53$, $p < .001$) but not in females ($N = 47$, $r_s = .25$, $p = .09$). D_{GO} was also associated with other behaviors beyond our

predictions. Gorillas scoring high on Dominance spent more time resting than gorillas scoring low on this dimension, and rates of staring and approaches were lower in gorillas scoring high on Dominance.

Insert Figure 2 about Here

Consistent with key traits of O_{GO} and our predictions, gorillas scoring high on this dimension had higher rates of staring and spent less time resting and immatures also spent more time playing. We also expected a positive correlation between O_{GO} and approach rates as well as the number of individuals within 5m but there was no association found. Instead, O_{GO} was negatively related to dominance strength of adult gorillas. Finally, the rate of touching was positively correlated with O_{GO}.

In line with our predictions, gorillas high on S_{GO} had more individuals in close proximity and higher approach rates. The rate of touching was not significantly correlated with S_{GO}. Also as expected, sociable subadult and adult gorillas spent more time grooming and had more grooming partners. Lastly, sociable gorillas spent less time resting during group resting periods.

As predicted, the fourth gorilla personality dimension, P-A_{GO}, was negatively related to rates of interventions. Contrary to our predictions, rates of aggression and rates of food stealing in subadult and adult gorillas were not significantly related to P-A_{GO}. Similar to more sociable gorillas, gorillas high on P-A_{GO} also spent less time resting, stared more frequently at other gorillas and had higher approach rates.

Discussion

Our main goal was to describe the personality structure of a wild habituated mountain gorilla population. The structure of wild mountain gorilla's personality included the dimensions Dominance, Openness, Sociability, and Proto-Agreeableness. These dimensions are associated with observed behaviors and had characteristics unique to gorillas and characteristics shared with other hominoids.

The inter-rater and internal consistency reliabilities of these dimensions and their traits are comparable to those found in studies of captive, semi-free, and free ranging nonhuman primates (Capitanio, 1999; King & Farmer, 2005; King & Figueredo, 1997; Konečná et al., 2008; Morton et al., 2013; Uher & Asendorpf, 2008; Weiss et al., 2007; Weiss et al., 2009, Weiss et. al., 2011), and also to those of facets (Costa & McCrae, 1992) or items (Kenrick & Stringfield, 1980) found in studies of humans. Yet, we cannot exclude rating biases due to previous discussions between about the animals, which is a possible problem of all personality studies based on ratings (Cicchetti, 1994).

Dominance

Like other primates (Freeman & Gosling, 2010), wild mountain gorillas possess a dimension associated with competitive prowess (D_{GO}). However, the gorilla variant differs from those of other apes and rhesus macaques in two respects. First, D_{GO} lacks an aggressive facet, a finding underpinned by a lack of an association between this dimension and rates of aggression. This suggests that aggressive features are not necessarily attributes of a dominant mountain gorilla. Secondly, D_{GO} incorporates traits (*protective*, *helpful*, and *sensitive*) that loaded on Agreeableness in other hominoids (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2006). This ‘supportive’ facet may be specific to Virunga mountain gorillas or it may be specific to gorillas more generally. This facet can be explained in terms of species-typical social

organization and the role of dominant males in gorilla social groups, which includes group protection and the mediation of within-group social conflicts (Schaller, 1963; Watts, 1996). Such an interpretation is further supported by clear links between D_{GO} and behavioral measures such as dominance strength and rates of interventions. Our findings also indicate that high-ranking females intervene more often than low-ranking females. Thus, high-ranking females may play a role similar to males in mediating within-group conflicts. However, the relationship between female dominance and female's social role within mountain gorilla groups is not well-understood and needs to be addressed in future studies. Our findings also revealed lower scores on D_{GO} in females than in males, as might be expected in the male-dominated mountain gorilla society. The absence of a 'supportive' facet in captive western lowland gorillas (Gold & Maple, 1994; Kuhar et al., 2006; Schaefer & Steklis, 2014) may be due to the lack of key circumstances in captivity, such as external threats from inter-group encounters or it may reflect the smaller number of traits assessed by the GBI.

Gorillas high on D_{GO} also stare less at other gorillas, have lower approach rates, spend more time resting and groom fewer group members. Although these associations were not predicted, they are consistent with certain aspects of mountain gorilla socio-ecology. In particular, staring in mountain gorillas has multiple functions and tends to be directed up the hierarchy (Yamagiwa, 1992). Also, given that dominant gorillas are responsible for group protection, resting may allow dominant individuals to monitor the group and environment. Finally, dominant gorillas are group leaders and are used as a reference to the group's center (Watts, 1985). Establishing strong bonds with the protectors of the group through close interactions is important for group members and may be reflected in higher approach rates and

grooming efforts towards dominant gorillas rather than vice versa (Harcourt & Stewart, 2007; Watts, 1992).

Our findings also indicate that among great apes, the absence of a broadly defined, distinct, dominance-like dimension (Digman, 1990; Goldberg, 1990) remains a unique feature of human personality (de Waal, 1995). This is not to say that narrowly defined lower-order dimensions or facets (Cattell & Mead, 2008; Costa & McCrae, 1995; Morrone-Strupinsky & Depue, 2004; Patrick, Fowles, & Krueger, 2009; Tellegen, 1982) related to dominance do not exist or cannot be found in humans. Indeed, studies have found elements related to agency, boldness, assertiveness, social dominance, ambition, and achievement in humans (Benning, Patrick, Blonigen, Hicks, and Iacono, 2005; McCrae, 1995; Morrone-Strupinsky & Depue, 2004; Patrick et al., 2009). However, these are specific to the particular instrument used in personality assessment and generally do not emerge in principal component or exploratory factor analyses of large batteries of items (Goldberg, 1990). Assessing humans using a version of the HPQ will rule out the possibility that the Dominance dimension is specific to the HPQ and not the species being rated. If such a study fails to identify a dominance-like dimension in humans, this would suggest that the lack of such as dimension is a unique feature of human personality.

There is growing evidence that differences between hierarchical societies of nonhuman great apes and humans reflect our evolutionary past as hunter-gatherers, including strong egalitarian tendencies, with social coalitions and alliances that span across a network of groups (Gavrilets, Duenez-Guzman, & Vose, 2008). Studies of personality structure in the more egalitarian bonobos (de Waal, 1995) are needed to determine whether the lack of Dominance, a seemingly unique feature of human personality, evolved through the selection of increasingly cooperative-egalitarian societies (Boehm, 1999; Weiss et al., 2011).

Openness

Consistent with our predictions, mountain gorilla personality structure includes an Openness dimension. O_{GO} was most similar to Openness found in brown capuchin monkeys (Morton et al., 2013) and rhesus macaques (Weiss et al., 2011), and to a lesser extend to the narrower variants in humans (Goldberg, 1990) and chimpanzees (King & Figueredo, 1997; Weiss et al., 2009) and to orangutan Extraversion. Orangutans are semi-solitary (Galdikas, 1985) and lack an Openness dimension (Weiss et al., 2006). Thus, these findings suggest that Openness benefits group-living primates with complex social systems.

The relatively stronger similarity of OGO to brown capuchin monkeys (Morton et al., 2013) compared to phylogenetically closer related great apes and rhesus macaques is difficult to explain. The activity facet in OGO may play a role therein as it is a key part of a distinct Activity dimension in rhesus macaques, which are believed to represent the common ancestor of catarrhines, and combines with sociability-related traits to create an Extraversion dimension in orangutans (Weiss et al., 2006), chimpanzees (King & Figueredo, 1997; Weiss et al., 2009), and humans (Goldberg, 1990). Mountain gorillas and brown capuchins lack a distinct Extraversion dimension, and traits describing activity merge with a facet that captures Openness (*curious, innovative*, *inquisitive*, and *inventive*) across primates.

The question remains as to why Activity is part of O_{GO} and not part of S_{GO} or Extraversion as in chimpanzees, humans, and orangutans? Activity combined with sociability may be a key feature of primates living in societies with high degrees of fission-fusion dynamics where group/party size and composition vary frequently (Aureli et al., 2008). Considering that our knowledge of orangutan personality is based on a captive population composed of Sumatran and Bornean orangutan species which exhibit different degrees of fission-fusion dynamics in the wild

(van Schaik, 1999), it would be valuable to investigate personality separately for each species. We predict that with increasing fission-fusion dynamics and complexity of social systems, Openness and extraverted Sociability (Extraversion) would become more distinct dimensions.

As predicted, O_{GO} combines three traits *curiosity*, *playful*, and *active*. Open gorillas had relatively high rates of staring and allocated less time to resting and more time to playing. Staring reflects curiosity but can also function as play solicitation in mountain gorillas (Yamagiwa, 1992). Furthermore, our findings demonstrate that O_{GO} captures behavioral variability among mountain gorillas even when excluding immature gorillas who are more active and playful and show greater curiosity within their environment. Playing, a key trait of O_{GO}, may remain important into early adulthood because of its role in developing social competence and forming long-term social bonds (Baldwin & Baldwin, 1974; Thompson, 1996), refining the neuromuscular system (Byers & Walters, 1995), and developing flexible kinematic and emotional responses to cognitively demanding situations (Spinka et al., 2001).

The predicted relationships between O_{GO} and rates of approach and proximity patterns were not supported. The lack of evidence for those relationships suggests that open gorillas socialize more opportunistically rather than actively seeking out social partners and/or that O_{GO} encompasses behaviors that do not require social interactions, including the exploration of new objects in the environment. An open gorilla may also frequently transfer between groups without developing close associations with group members.

Sociability

As predicted, mountain gorilla personality encompasses a dimension related to Sociability (S_{GO}) on which females score higher than males, reflecting the females' role in establishing bonds with males and caring for offspring (Fletcher, 1994; Harcourt & Stewart,

2007; Watts, 1992). Also consistent with our predictions, S_{GO} was directly related to time spent grooming, number of grooming partners, proximity pattern, and rates of approach. In contrast to humans and other great apes (Goldberg, 1990; King & Figueredo, 1997; Weiss, King & Perkins, 2006), mountain gorillas lack distinct Agreeableness and Extraversion dimensions. Instead, they possess a blend of these dimensions. The same pattern is found in rhesus and Barbary macaques whose personality structures may be representative of the common ancestor of catarrhines (Konečná et al., 2012; Weiss, Adams, & Perkins, 2006), and also in brown capuchin monkeys (Morton et al., 2013).

This pattern of hominoid personality dimensions raises intriguing questions. For example, what selection pressures favor separate Extraversion and Agreeableness dimensions? Independent Agreeableness and Extraversion dimensions may be favoured in primate species living in social systems with fission-fusion dynamics such as humans, chimpanzees, and orangutans (Aureli et al., 2008). The potential for spatio-temporal variation in cohesion and individual membership in groups of primates with fission-fusion dynamics may require more complex and flexible social and cognitive abilities (Aureli et al., 2008). The independence of Agreeableness and Extraversion offers more behavioral strategies to respond and adapt to varying ecological and social environments affecting costs and benefits of living in groups. This is supported by a study in humans showing that individual differences in Extraversion and Agreeableness are linked to variation in cooperative behaviour across different situations (Koole, Jager, van den Berg, Vlek, & Hofstee, 2001). For examples, extraverted and disagreeable participants followed a strategy that maximized their gain from collective sources across situations, while introverted and agreeable participants were more cooperative and sensitive to situational changes in the social environment and in collective resource availability. However,

fission-fusion dynamics may not be the only evolutionary driver of independent Agreeableness and Extraversion dimensions in primates as a blend of both dimensions was also found in brown capuchin monkeys (Morton et al., 2013) of which some populations live in a society with lower fission-fusion dynamics (Aureli et al., 2008).

Proto-Agreeableness

The reverse (multiply trait loadings by "-1") of gorilla 'Proto-Agreeableness' (P-A_{GO}) captured traits that are part of the negative pole of human Agreeableness (Goldberg, 1990) and of the positive pole of orangutan Dominance (Weiss et al., 2006). This dimension may stem from the lost aggressive-selfish facet in D_{GO} that is attached to Dominance in rhesus macaques and orangutans (Weiss et al., 2006; Weiss et al., 2011). The lack of covariance between aggressive-selfish behavioral tendencies and traits describing Dominance may highlight the relatively low importance of aggressive tendencies, particularly given the degree of sexual dimorphism, compared to supportive tendencies for gorilla dominance.

With the exception of dominance strength, the behaviors associated with P-AGO are the same, though in the opposite direction, as those related to D_{GO}. In other words, the correlations suggest that gorillas high on 'Proto-Agreeableness' share behaviors with low-ranking gorillas, but they are not necessarily low in the social hierarchy. Similar findings in humans show that high prominence, respect, and being influential are not related to Agreeableness (Anderson, John, Keltner, & Kring, 2001; Savin-Williams, 1979).

Similar to the orangutan (Weiss et al., 2006) and rhesus macaque (Weiss et al., 2011) personality structure, and indeed the personality structure of most non-primate species (Gosling & John, 1999), mountain gorilla personality lacks a dimension like human Conscientiousness (Goldberg, 1990). There is some indication that captive western lowland gorillas possess a

dimension like Conscientiousness (Schaefer & Steklis, 2014), but given the small sample size (8 individuals), additional data are needed to confirm those findings. To date, the hypothesis holds that Conscientiousness evolved recently within Homininae (Gosling & John, 1999). This does not mean that other primates and animals do not differ in behavioral tendencies that underpin Conscientiousness, such as determination, planning, order, and discipline (Gosling & John, 1999). Rather, it indicates that these tendencies are not as central in most animals' personalities and behavioral repertoires so as to be captured by a separate dimension. Selection for Conscientiousness within Homininae may be the emergence of cooperative hunting behavior, which takes a central role in hominid evolution and involves high levels of organization, timing, control, and, to some extent, delayed gratification (Boesch & Boesch, 1989). Alternatively, societies with strong reliance on social learning, tool use, and with distinct "cultural" traditions may play an important role in the evolution of Conscientiousness in primates (Morton et al., 2013) which is supported by close resemblances of Conscientiousness in organutan Intellect (Weiss et al., 2006) and in brown capuchin Attentiveness (Morton et al., 2013).

In line with our predictions that neurotic tendencies are less evident in species that live in stable and predictable environments, Neuroticism, which captures fearfulness, emotional reactivity, vulnerability to stress and excitability (Gosling & John, 1990), is absent in mountain gorillas. This contrasts with findings in humans and other great apes (Costa & McCrae, 1992; Digman, 1990; Goldberg, 1990; Weiss et al., 2009; Weiss et al., 2006). Studying personality of gorilla species along a gradient of increasing seasonal variation in food availability would be a strong test of this prediction.

Conclusions

Our findings highlight the insights into the proximate and ultimate bases of personality by merging approaches hailing from behavioral, ecology, personality psychology, and comparative psychology. Future studies, applying similar methods to study primates that span a range of social systems and ecological niches, are needed to understand the evolution of primate personality and its relationship with social and environmental factors. Studying personality variation across well-studied wild gorilla species and populations (Sousa & Casanova, 2005/2006) will open up new opportunities to better understand the interplay of behavior, ecology, social systems, and personality that is only partially elucidated by captive populations. Future comparative personality studies also have the potential to provide further insight into speciation processes and the role that personality plays in these processes (Uher, 2008; Weiss & Adams, 2013).

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Table 1

Predictions for dimension categories (see Freeman & Gosling, 2010) in Virunga mountain gorilla personality structure based on gorilla-/population-specific ecology and society ('+' expected, '-' not expected, 'empty' no prediction).

Ecological & social feature	Sociability	Confidence	Aggression	Fearfulness	Curiosity	Anxiousness	Playfulness	Activity	Excitability	Impulsivity	Dominance	Agreeableness	Irritability	Intelligence	Independence
Stable environment				-	-	-			-	-			-		
Low food competition / no territorial defence			-												
Cohesive social groups / lack of fission-fusion	+							-							
Strong male-female bonds	+														
Social role of males and females												+			
Hierarchical social system (dominance)		+									+			+	+
Male and female dispersal					+										

Table 2

Distribution of 116 study gorillas over all age-sex classes (see Table II in Breuer et al., 2009) with modified age-range of infants.

Age category	Age-range (year)	N females	N males	N Total
Full-grown silverback	>15	-	18	18
Young silverback	>12-15	-	6	6
Blackbacks	>8-12	-	8	8
Adult female	> 8.0	40	-	40
Sub-adult	> 6.0 – 8.0	7	7	14
Juvenile	> 3.5 – 6.0	9	6	15
Infant	1.0 – 3.5	4	11	15

Table 3

Behavioral categories and rules for recording each behavior.

Behavior	Definition	Recording rules	Data restricted to:
Aggression	An individual successfully or unsuccessfully tries to hit, shove, drag, kick, grab, chase or bite another individual in an agonistic manner often associated with a threatening face, such an open-mouth.	Continuous	Sub-/adults
Staring	An individual looks intently at another individual (or vice versa) at very close range between > 0-1 m.	Continuous	
Intervention	During an agonistic encounter, a previously uninvolved individual (the third party) ends a conflict between the two individuals engaged in an agonistic interaction by supporting any one individual or being neutral. This also includes intervention during food-stealing.	Continuous	Sub-/adults
Displacement	One individual moves away from another approaching individual when the approaching individual is within 2 m proximity. The retreat is in direct response to the approaching individual. This may include physical contact which should be recorded as a separate behavioral event. Actor and recipient are recorded.	Continuous	Adults
Food-stealing	An individual takes or tries to take a food item either directly from the hands or mouth of another or from a pile of food collected by another individual.	Continuous	Non-resting & Sub-/adults
Touching	An individual gently puts hands, fingers (not bent) or feet on another individual in an affiliate manner.	Continuous	
Approach	One individual moves to within 2 m of another individual and either remains within 2m for a minimum duration of 1 min or engages in an affiliative behavior. This behavior is not recorded during group travel periods.	Continuous	
Grooming	An individual picks through the hair of another individual with fingers or lips, removing dry skin, dirt, insects, etc. Actor and recipient are recorded.	Continuous / Instant	Resting & Sub-/adults
Playing	An individual engages in wrestling, chasing, sparring, and/or mock-biting with another individual. This category also includes infants playing on mother's body.	Instant	Immatures
Resting	The focal is inactive in one spot without actively engaging in social interactions.	Instant	Resting
Individuals within 5 m	Sum of group members within 0-5 m distance to the focal.	Instant	Resting

Table 4

Everett (1983) test of robustness of the four- and five dimension solutions.

	I	II	III	IV		Congruence
Infants excluded	0.98	0.99	0.99	0.99		0.99
Infants & Juveniles excluded	0.96	0.97	0.98	0.95		0.99

	I	II	III	IV	V	Congruence
Infants excluded	0.98	0.99	0.99	1.00	0.99	0.99
Infants & Juveniles excluded	0.97	0.98	0.97	0.99	0.86	0.96

Table 5

Traits loading on gorilla personality dimensions ($_R$ reflected) derived from a PCA with varimax rotation including 116 gorillas compared to other great apes.

				Gorilla				
Trait	**HU**	**CH**	**OR**	**D_R**	**O**	**S**	**P-A_R**	**h^2**
Intelligent	+O[a]	+D[d]	+I[f]	**0.91**	-0.09	0.05	-0.17	0.86
Decisive	+C[a]	+D[d]	+I[f]	**0.81**	-0.22	-0.13	-0.20	0.77
Protective	+A[b]	+A[d]	+A[f]	**0.81**	-0.16	-0.07	-0.39	0.83
Timid	-E[a,c]	-D[d]	+N[f]	**-0.80**	-0.36	0.05	0.07	0.78
Anxious	+N[a,c]	-D[e]	+N[f]	**-0.78**	-0.36	0.04	-0.24	0.79
Independent	-N[a]	+D[d]	+I[f]	**0.77**	-0.25	-0.37	-0.24	0.84
Dominant	+E[a,c]	+D[d]	+D[f]	**0.75**	-0.25	-0.14	**-0.45**	0.85
Fearful	+N[a]	-D[d]	+N[f]	**-0.73**	0.03	0.05	-0.21	0.58
Sensitive	+A[a]	+A[d]	+A[f]	**0.72**	-0.36	0.27	-0.08	0.73
Distractible	----	----	----	**-0.71**	**0.44**	0.35	0.10	0.83
Helpful	+A[a]	+A[d]	+A[f]	**0.68**	-0.31	0.29	-0.32	0.75
Bullying	-A[b]	+D[d]	+D[f]	**0.64**	0.15	-0.29	-0.57	0.83
Dependent	+N[a]	-D[d]	-I[f]	**-0.63**	0.33	**0.40**	0.25	0.73
Disorganized	-C[a]	-C[d]	-I[f]	**-0.62**	**0.55**	-0.05	0.07	0.68
Submissive	-E[c]/+N[a]	-D[d]	-D[f]	**-0.61**	-0.19	0.32	0.28	0.59
Imitative	-O[b]	+E[d]	+E[f]	**-0.60**	**0.53**	0.39	0.26	0.87
Persistent	+C[a]	+D[d]	+D[f]	**0.55**	0.22	-0.16	**-0.47**	0.60
Clumsy	----	-C[e]	+I[f]	**-0.54**	0.09	-0.03	-0.02	0.30
Vulnerable	+N[c]	-D[e]	+N[f]	**-0.53**	0.31	-0.16	0.15	0.42
Active	+E[a]	+E[d]	+E[f]	-0.10	**0.83**	0.21	0.27	0.81
Cool	-E[a]	-N[e]	-N[f]	0.23	**-0.77**	0.27	0.22	0.77
Thoughtless	-C[c]/-A[a]	-C[e]	----	-0.20	**0.77**	-0.15	-0.12	0.66
Unemotional	-N[a,c]	-N[d]	-E[f]	-0.08	**-0.76**	-0.11	-0.05	0.60
Playful	+E[a]	+E[d]	+E[f]	-0.40	**0.75**	0.35	0.27	0.91
Impulsive	+E[a]	-C[d]	+N[f]	-0.07	**0.74**	-0.07	-0.35	0.68
Lazy	-C[a]	-E[d]	-E[f]	-0.23	**-0.73**	-0.12	-0.25	0.67
Curious	+O[a]	+O[e]	+E[f]	-0.38	**0.73**	0.36	0.07	0.81
Inventive	+O[a]	+O[d]	+E[f]	-0.08	**0.70**	0.22	-0.21	0.59
Excitable	+N[a]	+N[d]	+N[f]	-0.12	**0.70**	-0.11	-0.37	0.64
Inquisitive	+O[a]	+O[d]	+E[f]	-0.31	**0.68**	0.36	0.05	0.69
Reckless	-C[a]	-C[d]	+D[f]	-0.09	**0.63**	-0.25	**-0.50**	0.72
Innovative	+O[a]	+O[e]	----	0.14	**0.62**	0.08	-0.22	0.46
Stable	-N[a]	-N[d]	-N[f]	0.27	**-0.61**	0.31	0.13	0.56
Conventional	-O[e]/-C[a]	+A[e]	-E[f]	0.05	**-0.60**	0.36	0.19	0.53
Quitting	-C[c]	-C[e]	----	-0.48	**0.60**	0.14	0.14	0.64
Erratic	-C[a]	-C[d]	+N[f]	-0.25	**0.57**	-0.38	-0.27	0.60
Predictable	+C[a]	+C[d]	-N[f]	-0.24	**-0.48**	0.41	0.03	0.46
Cautious	+C[a]	-D[d]	+N[f]	0.07	-0.37	-0.14	-0.32	0.26
Friendly	+A[a]	+E[d]	+A[f]	-0.21	0.12	**0.87**	0.22	0.86
Sociable	+E[a,c]	+E[d]	+A[f]	-0.01	0.27	**0.85**	-0.17	0.82
Affectionate	+A[a]	+E[d]	+A[f]	0.03	-0.04	**0.82**	0.03	0.68
Solitary	-E[b]	-E[d]	-E[f]	0.15	-0.12	**-0.81**	-0.07	0.70
Depressed	-E[b]	-E[d]	-E[f]	-0.08	-0.33	**-0.76**	-0.18	0.72
Gentle	+A[b]	+A[d]	-D[f]	-0.14	-0.22	**0.68**	**0.43**	0.70
Sympathetic	+A[a]	+A[d]	+A[f]	0.38	-0.36	**0.63**	-0.06	0.68
Defiant	-A[b]	-C[e]	+D[f]	0.31	0.23	**-0.61**	**-0.51**	0.77

Individualistic	-N[a]	-E[e]	----	0.34	0.03	**-0.55**	**-0.48**	0.64
Jealous	-A[a]/+N[a,c]	-C[d]	+D[f]	0.15	0.12	-0.12	**-0.85**	0.77
Irritable	-A[a,c]	-C[e]	+D[f]	0.17	0.18	**-0.42**	**-0.75**	0.81
Aggressive	-A[a]	-C[d]	+D[f]	0.35	0.11	**-0.48**	**-0.71**	0.87
Stingy	-A[a,c]	+D[d]	+D[f]	0.45	-0.07	-0.23	**-0.68**	0.72
Manipulative	-A[a]	+D[e]	+D[f]	0.31	-0.27	0.28	**-0.53**	0.53
Autistic	----	nl	nl	-0.01	0.13	-0.05	-0.29	0.11
% variance				21	21	15	11	

Note. Boldface = salient loadings; nl = no loading; '----' = trait (or included term) not assessed; '+' = positive loadings; '-' = negative loadings; h^2 communality; E = Extraversion (facets: sociability, assertiveness, activity, positive emotions[g]); C = Conscientiousness (facets: deliberation, self-discipline, dutifulness, order[g]); O = Openness (facets: ideas/intellect, imagination, creativity, curiosity[g]); N = Neuroticism (facets: anxiety, depression, vulnerability to stress, moodiness[g]); A = Agreeableness (trust, tender-mindedness, cooperation, lack of aggression[g]); D = Dominance (nonhuman great apes); I = Intellect (orangutan); HU = human, CH = chimpanzee, OR = orangutan.

[a] traits (or synonyms of traits) and classification (Goldberg, 1990)

[b] traits and their classification (Goldberg, 1990) as described in Table 1 (King & Figueredo, 1997)

[c] traits and their classification (McCrae & Costa, 1987)

[d] traits and their classification (King & Figueredo, 1997)

[e] traits and their classification (Weiss et al., 2008)

[f] traits and their classification (Weiss et al., 2006)

[g] for more details see John (1990) and Costa & McCrae (1992)

Table 6

Correlations between unit-weighted scores as defined by the mountain gorilla, chimpanzee (1: King & Figueredo, 1997; 2: Weiss et al., 2008), orangutan (Weiss et al., 2006), rhesus macaque (Weiss et al., 2010), brown capuchin monkey (Morton et al., 2013) personality structure.

	Gorilla			
	I	II	III	IV
Chimpanzee1				
Dominance	**0.97 (0.96, 0.98)**	-0.23 (-0.40, -0.05)	**-0.36 (-0.51, -0.19)**	**-0.65 (-0.75, -0.53)**
Extraversion	**-0.54 (-0.66, -0.39)**	**0.52 (0.38, 0.64)**	**0.84 (0.78, 0.89)**	**0.48 (0.32, 0.61)**
Conscientiousness	0.18 (-0.01, 0.35)	**-0.78 (-0.01, -0.35)**	**0.40 (-0.84, -0.70)**	**0.44 (0.28, 0.58)**
Agreeableness	**0.62 (0.49, 0.72)**	**-0.56 (-0.67, -0.42)**	**0.35 (0.18, 0.01)**	-0.13(-0.30, 0.06)
Neuroticism	-0.20 (-0.37, -0.02)	**0.82 (0.75, 0.87)**	-0.18 (-0.35, 0.01)	-0.23 (-0.39, -0.05)
Openness	**-0.41 (-0.55, -0.24)**	**0.86 (0.81, 0.90)**	0.27 (0.09, 0.43)	0.16 (-0.02, 0.34)
Chimpanzee2				
Dominance	**0.97 (0.95, 0.98)**	-0.22 (-0.39, -0.04)	**-0.42 (-0.56, -0.26)**	**-0.66 (-0.75, -0.54)**
Extraversion	**-0.51 (-0.63, -0.36)**	**0.57 (0.43, 0.68)**	**0.81 (0.74, 0.87)**	**0.44 (0.28, 0.57)**
Conscientiousness	-0.21 (-0.37, -0.02)	**-0.53 (-0.65, -0.39)**	**0.61 (0.48, 0.71)**	**0.73 (0.63, 0.81)**
Agreeableness	**0.67 (0.55, 0.76)**	**-0.49 (-0.61, -0.33)**	**0.31 (0.13, 0.47)**	-0.18 (-0.35, 0.00)
Neuroticism	-0.21 (-0.38, -0.03)	**0.82 (0.75, 0.87)**	-0.11 (-0.29, 0.07)	-0.17 (-0.34, 0.01)
Openness	**-0.39 (-0.53, -0.22)**	**0.81 (0.74, 0.87)**	**0.26 (0.08, 0.42)**	0.14 (-0.14, 0.31)
Orangutan				
Extraversion	**-0.53 (-0.65, -0.39)**	**0.85 (0.79, 0.89)**	**0.51 (0.36, 0.64)**	**0.33 (0.16, 0.49)**
Dominance	**0.72 (0.62, 0.80)**	0.04 (-0.14, 0.22)	**-0.62 (-0.72, -0.49)**	**-0.93 (-0.95, -0.90)**
Neuroticism	**-0.54 (-0.65, -0.39)**	**0.67 (0.56, 0.76)**	-0.25 (-0.42, -0.07)	-0.11 (-0.28, 0.08)
Agreeableness	**0.40 (0.23, 0.54)**	**-0.24 (-0.40, -0.06)**	**0.64 (0.52, 0.74)**	-0.06 (-0.24, 0.12)
Intellect	**0.96 (0.94, 0.97)**	**-0.47 (-0.60, -0.32)**	**-0.36 (-0.51, -0.19)**	**-0.50 (-0.63, -0.35)**
Rhesus macaque				
Confidence	**0.93 (0.89, 0.95)**	**-0.47 (-0.60, -0.31)**	-0.25 (-0.41, -0.07)	**-0.42 (-0.56, -0.26)**
Openness	**-0.49 (-0.62, -0.34)**	**0.92 (0.89, 0.95)**	0.23 (0.05, 0.39)	0.17 (-0.01, 0.34)
Dominance	**0.74 (0.64, 0.81)**	0.02 (-0.16, 0.20)	**-0.68 (-0.77, -0.57)**	**-0.91 (-0.94, -0.87)**
Friendliness	**0.50 (0.35, 0.63)**	-0.16 (-0.33, 0.02)	**0.59 (0.46, 0.70)**	-0.15 (-0.32, 0.04)
Activity	**-0.34 (-0.49, -0.16)**	**0.90 (0.86, 0.93)**	**0.18 (0.00, 0.35)**	0.20 (0.02, 0.37)
Anxiety	**-0.41 (-0.55, -0.24)**	**0.81 (0.73, 0.86)**	-0.17 (-0.34, 0.01)	-0.25 (-0.41, -0.07)
Brown Capuchin				
Assertiveness	**0.87 (0.81, 0.91)**	-0.10 (-0.28, 0.09)	**-0.55 (-0.67, -0.41)**	**-0.86 (-0.90, -0.80)**
Openness	**-0.34 (-0.49, -0.17)**	**0.94 (0.92, 0.96)**	0.18 (-0.01, 0.35)	0.10 (-0.08, 0.28)
Neuroticism	**-0.38 (-0.53, -0.21)**	**0.86 (0.80, 0.90)**	**-0.22 (-0.38, -0.03)**	-0.11 (-0.28, 0.08)
Sociability	-0.20 (-0.37, -0.02)	0.19 (0.00, 0.36)	**0.93 (0.90, 0.95)**	**0.34 (0.17, 0.50)**
Attentiveness	**0.76 (0.67, 0.83)**	**-0.77 (-0.84, -0.69)**	-0.01 (-0.19, 0.17)	-0.25 (-0.42, -0.07)

Note. Significant effects at $p < .05$. (boldface). 95% confidence intervals in brackets.

Table 7

Inter-rater reliabilities of gorilla personality dimensions.

Dimension	*ICC*(3,1)	*ICC*(3,*k*)	Cronbach's α
I	0.69	0.92	0.95
II	0.41	0.77	0.94
III	0.45	0.80	0.92
IV	0.42	0.78	0.88

Table 8

Output of regressions examining age and sex effects on mountain gorilla personality dimensions using z-scores.

Dimension	Predictors	*b*	SE_b	*t*	*p*
Dominance	Age	0.449	0.105	4.284	<0.001
	Sex	0.050	0.007	7.377	<0.001
	Age x Sex	0.079	0.011	7.064	<0.001
Openness	Age	0.489	0.147	3.323	0.001
	Sex	-0.040	0.010	-4.216	<0.001
	Age x Sex	-0.035	0.016	-2.263	0.026
Sociability	Age	-0.597	0.167	-3.582	<0.001
	Sex	-0.046	0.011	-4.289	<0.001
	Age x Sex	-0.006	0.018	-0.344	0.732
Proto-Agreeableness	Age	-0.154	0.164	-0.936	0.351
	Sex	-0.049	0.011	-4.604	<0.001
	Age x Sex	-0.015	0.017	-0.854	0.395

Table 9

Spearman's rank correlations between behavioral measures and trait dimensions.

Behavioral measure	*n*	Dominance	Openness	Sociability	Proto-Agreeableness
Dominance strength	58	0.65*	-0.45*	0.02	-0.01
Intervention per hour	86	0.32*	-0.14	0.04	-0.35*
Staring per hour	116	-0.57*	0.39*	0.43*	0.35*
% Playing	30	-0.26	0.60*	0.27	0.26
% Resting	116	0.58*	-0.28*	-0.51*	-0.37*
% Grooming	86	-0.12	-0.29	0.33*	0.00
N Grooming Partners	86	-0.07	0.01	0.41*	0.15
Mean N Gorillas ≤ 5 m	116	-0.04	-0.10	0.28*	-0.07
Touching per hour	116	-0.10	0.27*	0.17	0.15
Approaches per hour	116	-0.66*	0.18	0.55*	0.36*
Aggression per hour	86	0.18	-0.31	0.22	-0.10
Food-stealing per hour	86	0.09	-0.02	0.06	-0.10

Notes. * Correlations significant at $p < .004$.

Figure 1

Score distribution of female (circle) and male (triangle) gorillas on each mountain gorilla personality dimension presented by gorilla age.

Figure 2

Relationship between gorilla Dominance scores and dominance strength.